Nature Conservation

Nature Conservation 54: 121–147 (2023)
DOI: 10.3897/natureconservation.54.105606

Research Article

Exploring life-history traits of an endangered plant (*Vicia biennis* L.) to support the conservation of marginal populations

Anett Endrédi[1], Ármin Sőth[2], Dóra Ércz[3], Balázs Deák[4], Orsolya Valkó[4], János György Nagy[5,6]

1 *Institute of Aquatic Ecology, HUN-REN Centre for Ecological Research, Karolina út 29., H-1113 Budapest, Hungary*
2 *Eötvös Loránd University, Egyetem tér 1-3, H-1053 Budapest, Hungary*
3 *Bio Garancia Kft, Dereglye u. 5/2, H-1036 Budapest, Hungary*
4 *'Lendület' Seed Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotány utca 2-4, H-2163 Vácrátót, Hungary*
5 *Hungarian University of Agriculture and Life Sciences, Doctoral School of Biological Sciences, Páter Károly u. 1., H-2100 Gödöllő, Hungary*
6 *Hungarian Research Institute of Organic Agriculture, Miklós tér 1., H-1033, Budapest, Hungary*

Corresponding author: Anett Endrédi (anett.endredi@gmail.com)

Abstract

We aimed to investigate the reproduction-related traits of *Vicia biennis* L., an endangered and poorly known wetland species in its western marginal populations (in Hungary), and discuss the conservational and ecological implications. We measured the mass, viability, and physical dormancy of half-year-old seeds in five in-situ collected seed lots, while potential seed longevity (i.e., seed bank type) was estimated from repeatedly germinating subsamples from four ex-situ collected seed lots for 3–8 years. Plant survival, flowering, and seed production were studied in different light-, irrigation-, and competition conditions in a botanical garden experiment. We found that 1) half-year-old seeds have a high germination capacity (78–100%), 2) and high level of physical dormancy (72–100%) in all examined Hungarian populations, and 3) the seeds can preserve their germination capacity for more than five years, although their viability sharply decreases, probably falling below 10% within ten years, when they are stored at room temperature. The results of the botanical garden experiment suggested that 1) the species is annual, not biennial; 2) it shows strong sensitivity to precipitation and low competitiveness for water; and 3) it can produce hundreds of seeds even in suboptimal (dry or shady) conditions. Although the species was found to be well-adapted to a temporally heterogeneous environment, its future vulnerability can increase depending on the duration of dry seasons. Further investigation of genetic diversity and soil seed bank is needed to estimate the actual vulnerability of the species while strengthening the populations through seed sowing, and additional vegetation control in the habitats is suggested.

Key words: Fabaceae, germination, physical dormancy, seed longevity, seed production

OPEN ACCESS

Academic editor: Peter Poschlod
Received: 27 April 2023
Accepted: 7 October 2023
Published: 7 December 2023

ZooBank: https://zoobank.org/C4116311-F458-42A1-B802-E22203752418

Citation: Endrédi A, Sőth Á, Ércz D, Deák B, Valkó O, Nagy JG (2023) Exploring life-history traits of an endangered plant (*Vicia biennis* L.) to support the conservation of marginal populations. Nature Conservation 54: 121–147. https://doi.org/10.3897/natureconservation.54.105606

Copyright: © Anett Endrédi et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Recently, several studies have shown that human-induced loss, fragmentation, and degradation of natural habitats, together with accelerating climate change, are among the most important drivers of current and future biodiversity crisis (Sala et al. 2000; Jaureguiberry et al. 2022). These processes may also

significantly affect species distribution patterns (Parmesan and Yohe 2003), leading to a significant level of species turnovers and species extinctions in several regions, such as the Pannonian region (Thuiller et al. 2005)).

An increasing number of models were developed to predict the responses of species and communities to future environmental changes in order to prioritize conservation actions (Thuiller et al. 2008). There is a growing demand for using trait-based approaches in plant ecology and related sciences (Violle et al. 2007) as well as in species distribution modelling (Violle and Jiang 2009; Violle et al. 2014). This approach needs high-quality functional trait data of the target species, which led to the development of large trait databases, e.g., TRY (Kattge et al. 2011), SID (Anon 2020) or LEDA (Kleyer et al. 2008). Although these databases have achieved unprecedented coverage (Kattge et al. 2020), there are still some critical knowledge gaps: seed-related traits except for seed mass (Jiménez-Alfaro et al. 2016; Saatkamp et al. 2019), and generally, the traits of rare species (Kattge et al. 2020) are surprisingly underrepresented in these databases and the literature.

Life history traits of rare plant species are often poorly known, and the relative importance of these species in maintaining ecosystem functioning has been underestimated for a long time (Grime 1998). However, several studies have shown that rare species often support important and vulnerable ecosystem functions (Lyons et al. 2005; Mouillot et al. 2013) as they are usually characterized by unique functional trait combinations in the given community (Jain et al. 2014). Furthermore, they potentially have an essential role in stabilizing food webs (Säterberg et al. 2019) and can even strengthen a community's resistance to invasions (Lyons and Schwartz 2001). Consequently, their role in maintaining ecosystem functioning and ecosystem services can be significant despite their small number in the community (Dee et al. 2019). However, rare species are considered more vulnerable to climate change, habitat loss, disturbance, or biological invasions; thus, their loss can contribute disproportionally to the current extinction crisis (Pimm et al. 1988; Enquist et al. 2019).

For the effective in-situ and ex-situ conservation of rare species, it is essential to have a basic knowledge of life-history traits related to germination and seedling establishment that can considerably affect population growth and stability (Saatkamp et al. 2019; Pence et al. 2022). This knowledge is also inevitable for planning effective reintroductions of rare species (Godefroid et al. 2011) and fundamental in the case of annual and biennial plants for which recruitment by seed is a crucial process due to their short life-cycle.

This study aimed to examine the life strategy of a poorly known, endangered plant species (*Vicia biennis* L.) and its reproduction-related traits in order to reveal potential sources of the species' vulnerability and understand its current demography and distribution.

Vicia biennis L. is a wild legume species with a 1–3m long, branching and climbing herbaceous stem system. Originally it was described as a biennial (hemitherophyte) plant, which is preserved in its Latin name, but recently, this was questioned in the literature. Nowadays, it is occasionally referred to as annual (Leht 2005; Király 2009), annual/biennial (Lesku and Molnár 2007; POWO 2023) or as a perennial liana with "periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface" (Botta-Dukát et al. 2023).

Although the species has a wide distribution area (from Hungary to Kazakhstan), its known populations are often isolated and situated far from each oth-

er. They live near wetland habitats: edge of gallery forests, willow bushes, or reed-framed watersheds in the steppe zone. These habitat types are profoundly affected by land use, climatic changes, and invasive alien species (Stohlgren et al. 1998; Schindler et al. 2016). According to Soó (1980), its habitats are characterised by moist, compacted clay or alluvial soils.

The westernmost populations live in the Pannonian Biogeographic Region in Hungary, where the species is endangered and strictly protected by law (Király 2007). It was probably always rare in this country and was among the first plants proposed for protection in 1908 (Farkas 1999). Herbarium specimens from the 1900s are sporadic (Molnár et al. 2000), but new populations have been found continuously since the late 1990s. In the last 25 years, 13 populations have been recorded in the "Vascular Plants of Hungary online database" (Fig. 1) (Bartha et al. 2023). These populations were found along the River Tisza and its tributaries, but not necessarily in wetland habitats. For example, Somlyay and Bauer (2013) found larger populations in near-water fallows and even in dry, weedy hay meadows, suggesting that the plant may not be strongly associated with wetlands, or at least, it can appear intermittently on drier habitat types too. According to the different ecological indicators collected together in the Pannonian Database of Plant Traits (Sonkoly et al. 2022), *Vicia biennis* is a disturbance-tolerant species and prefers moist, sunny/semi-shaded and nitrogen-rich habitats (Soó 1980; Borhidi 1995).

The size of the found populations was highly variable, ranging from one specimen to more than 100 individuals. However, despite all conservational efforts, this shows a high within-population variation between years. Based on this and the vulnerability of wetland habitats, the species was suggested for ex-situ conservation by the Hungarian National Park Directorates (Házi and Lesku 2006), and an ex-situ population was established in 2009 in the MATE botanical garden, Gödöllő (Fig. 1).

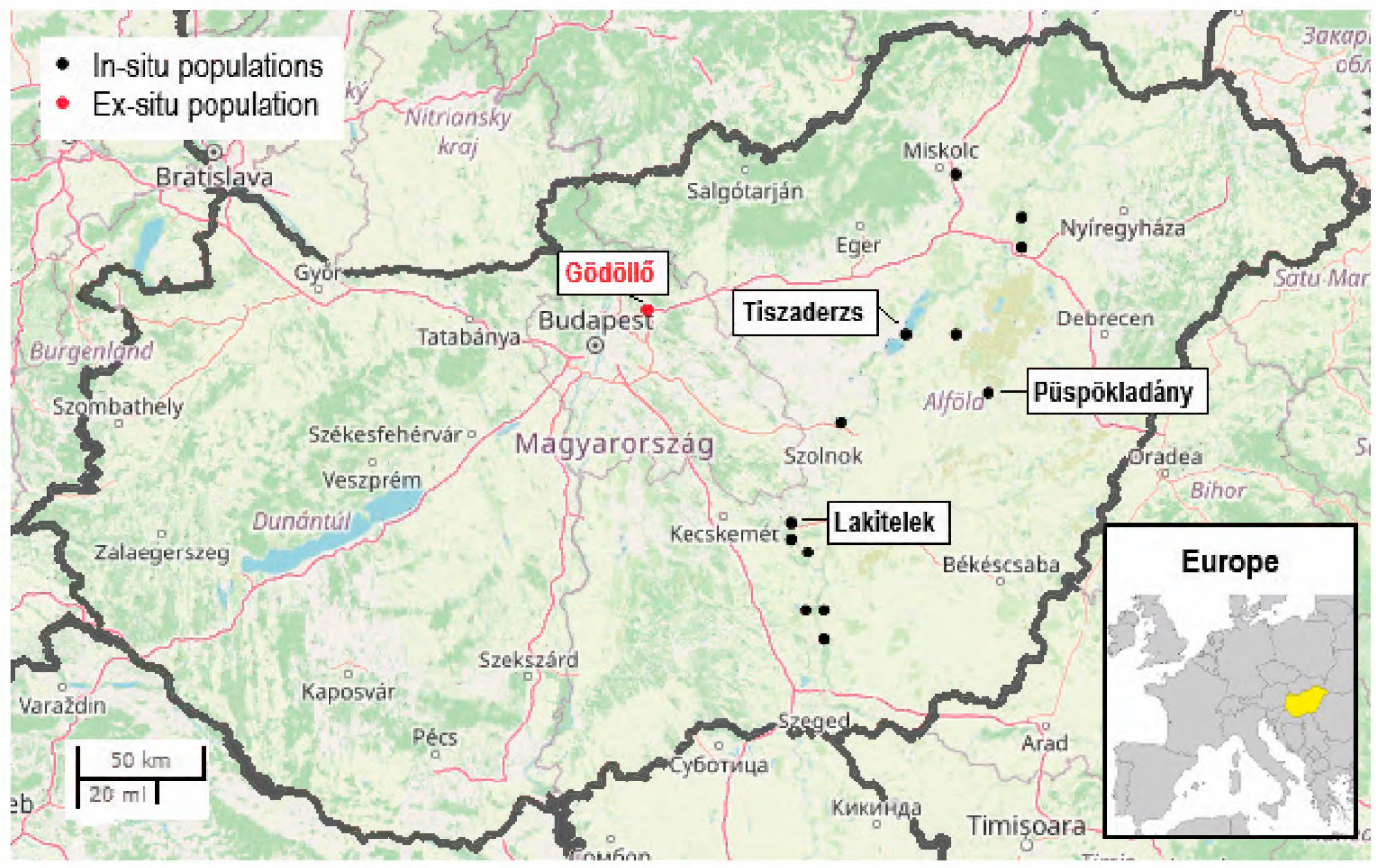

Figure 1. Location of the ex-situ and in-situ populations in Hungary validated after 1990. Examined populations (Tiszaderzs, Püspökladány and Lakitelek) are highlighted. The map is based on the data of the Vascular Plants of Hungary online database (Bartha et al. 2023).

Despite the species' endangered conservation status, vulnerability, and its well-known crop (e.g., *Vicia sativa*) and weed (e.g., *V. cracca*) relatives, only morphological data and no functional trait data are available about *V. biennis* in the literature or public databases (e.g., SID (Anon 2020), TRY (Kattge et al. 2020)), making predictions and conservation actions even more challenging.

In our research, we aimed to experimentally investigate some reproduction-related traits of the species in semi-natural conditions: Seed and germination-related traits (i.e., seed mass, potential seed longevity, dormancy, germination capability) were examined in greenhouse experiments, while plant survival, flowering, seed production and their reaction to different light exposure and precipitation were investigated in a botanical garden experiment. The main questions and hypothesis of the study were the followings:

1) What is the degree and variance of mass, physical dormancy, and germination capacity (viability) of seeds collected from different in-situ populations?

A vast majority of species in the Fabaceae family produce seeds with some kind of dormancy – mostly physical (PY) or combinational (i.e., physical + physiological, PY+PD) dormancy (Baskin and Baskin 1998; Van Assche and Vandelook 2010; Jayasuriya and Wijetunga 2013). The primary role of physiological dormancy (PD) is to inhibit germination until environmental conditions are favourable for seedling establishment (e.g., waiting for the end of the summer period in the case of winter annuals (Van Assche and Vandelook 2010)). In contrast, seeds with physical dormancy (PY) cannot germinate even in favourable conditions until their water-impermeable structures in the seed coat break due to mechanical or thermal effects (Baskin and Baskin 2004; Renzi et al. 2014). From a long-term conservational perspective, physical dormancy (PY) can be more important in the bet-hedging of annual or biennial species and greatly impact population dynamics, as it can positively correlate with the seeds' longevity as well as delay germination for many years. (Cohen 1966; Childs et al. 2010).

Due to the limited number of seeds available from the endangered populations of *V. biennis*, we decided not to test all potential dormancy types but rather focus on the more important physical dormancy (PY). Based on the expected life form of the species (i.e., summer annual) and the seed characteristic of other *Vicia* species, high between-population variances in seed dormancy, weight, and viability were expected. As the examined in-situ populations are small and variable (containing ~10–50 individuals), detecting signs of inbreeding depression (e.g., low viability of seeds) was also conceivable.

2) What is the potential seed longevity (seed bank type) of *Vicia biennis*? How long can the seeds potentially preserve their germination capacity?

The longevity of seeds (i.e., the time they can preserve their germination capacity) is a crucial seed trait affecting the survival of endangered, annual/biennial plant populations. Although this highly depends on the species' attributes, environmental conditions affect it too (Bekker et al. 2003). For the effective conservation of a species, maximum ex-situ seed longevity (i.e., the time the seeds can be stored in controlled conditions without losing their germination

capacity), potential in-situ seed longevity (i.e., the time the seeds can persist in the soil without losing their germination capacity) and realized in-situ seed longevity (i.e., the actual seed longevity on a given habitat) can be all important. Ex-situ seed longevity is usually measured by controlled seed ageing experiments (Newton et al. 2014), while long-term seed burial experiments can help to estimate in-situ seed longevity (e.g., Csontos et al. 2016). The former is more expensive and requires proper lab equipment, while the latter is time-consuming and highly affected by the soil and weather conditions. In addition, both approaches require hundreds/thousands of seeds, which can be problematic for an endangered species. In a simplified approach, seed longevity can also be estimated by ecological correlates (Probert et al. 2009): e.g., in-situ seed persistence is correlated with some seed characteristics (mass, shape, and density in the soil) (Thompson et al. 1993; Bekker et al. 1998). However, these simplified approaches are usually limited only to determine the potential seed bank type of the species, i.e., if a species probably has a transient seed bank (with seeds viable for less than one year), a short-term persistent seed bank (with seed persistence between 1–5 years) or a long-term persistent seed bank (with seeds preserving their viability for more than five years) (Thompson 1993).

Although we did not have the conditions (lab and a sufficient number of seeds) to conduct a proper longevity test, we wanted to estimate at least the potential seed bank type of the species by testing the viability of seeds with different ages in the short-term ex-situ seed collection. Based on the known ecological correlates, it is not clear what seed bank type to expect: E.g., species with similarly large seed sizes have a higher chance to have a short-lived, transient seed bank (Csontos 2001) but short life histories (e.g., annual life form) are usually associated with increased seed persistence in soils (Thompson et al. 1998).

3) How do light, precipitation, and root competition affect mortality, growth, flowering, and seed production?

V. biennis often grows close to wetland habitats in the half-shaded edge of taller vegetation (e.g., bushes or cattails); thus, we hypothesized that the species has a relatively low light requirement and high water demand for healthy development and seed production.

Materials and methods

Examined populations

Three in-situ and one ex-situ Hungarian population were selected as seed sources to study the seed traits of the species (Fig. 1).

The Tiszaderzs population was found in 1999, near a canal connected to an oxbow of the River Tisza (Cserőközi-Holt-Tisza). At that time, the known habitats of the species were threatened by invasive weeds (e.g., *Amorpha fruticosa*, *Vitis* spp., *Echinocystis lobata*, *Solidago gigantea)* (Molnár et al. 2000). In 2009, the individuals occurred 20–50 m from the canal, mainly in a young, semi-shaded poplar forest (*Populetum canadensis cultum*) in the neighbourhood of a holiday home zone. However, a few individuals had already appeared in the more open willow bushes (*Calamagrosti – Salicetum cinereae*) nearby. Regarding the

vegetation, although we found some typical softwood gallery forest species (e.g., *Salix alba*, *Rubus fruticosus*, *Galium mollugo*) in the forest habitat, most of the recorded plants were disturbance-tolerant weeds (e.g., *Amaranthus albus*, *Cirsium vulgare*, *Artemisia vulgaris*, *Tanacetum vulgare*, *Equisetum arvense*) and *V. biennis* had to cope with many invasive neophytes (e.g., *Conyza canadensis*, *Erigeron annuus*, *Amorpha fruticosa*) too (Endrédi 2010; Endrédi and Nagy 2012). Between 2009 and 2016, the estimated population size oscillated between 40 and 5 individuals (Endrédi 2012; Sőth 2017).

In the last decade, the forest habitat has become more shaded, and despite all conservational efforts (e.g., early spring weed control and some reintroduction attempts), the number of *V. biennis* individuals showed a significant decrease here. Meanwhile, the shift of the population towards the continuously disturbed (cut) edge of willow bushes was observed.

The Püspökladány population was found in 2009 in a ditch between fields. Here, the plant community was mainly composed of typical wetland species (e.g., *Typha angustifolia*, *T. latifolia*, *Bolboschoenus maritimus s. l.*, *Lycopus exaltatus*, *Butomus umbellatus*) (Gulyás 2013). Two years later, in 2011, the population size was about a dozen (Gulyás 2013), and we found a similar number (10–15) of individuals in the year of the seed collection (2015), climbed up to cattail (*Typha spp*). We do not have information about the conservation of this population.

The Lakitelek population was recorded in 2012. A few dozen individuals occurred on a pond's steep shore, and a similar number of plants were found nearby, on the embankment between artificial ponds (Somlyay and Bauer 2013). In 2014, we found about 10–15 plants climbed up to the vegetation on the edge of a pond. In 2017 and 2018, we did not find the species here, while the cover of disturbance-tolerant weeds has increased dramatically. Although, on the edge of a nearby artificial pond, a few dozen individuals appeared in 2017 (Ércz 2018).

The ex-situ population was established in 2009 in the Botanical Garden of MATE (Gödöllő). For the establishment, seeds were collected from the Tiszaderzs population in 2007 and germinated in 2009. The species' preference for light and moist conditions was tested in the first year. The results and the conditions are presented in this paper. In the following years, the population was maintained partly by spontaneous germination and partly by additional seed sowing and seedling planting. All seeds/plants used for the sowing and plantation originated from the previous seed lots of the same ex-situ population. The number of seed-producing individuals in this population varied between 50 and 100, and about 50% of the mature seeds was collected each year.

Seed collection and storage

In the germination tests, we used both in-situ and ex-situ collected seeds. In this paper, we will use the term "seed lot" for seeds collected from the same population in the same year, while "seed sample" refers to subsamples of seed lots for germination experiments or weighing.

Five in-situ seed lots were collected in four years (2013, 2014, 2015, 2017) from the three different populations (Fig. 1): Tiszaderzs (13T and 14T), Lakitelek (14L and 17L) and Püspökladány (15P). In the years of seed collections, all populations contained only a relatively small number of individuals: The Tiszaderzs population contained approximately 40 individuals, the Lakitelek

population was formed by 10–15 (2014) and 20–30 (2017) individuals, while the Püspükladány population included only 10–15 individuals. Population size was estimated partly by counting the stems right above the ground and partly based on the more or less separated canopies, as in some cases, the vegetation density (dense willow bushes, cattail or the "carpet" formed by the target species) made it impossible to count each stem separately.

We performed only one seed collection in a vegetation season to minimize the disturbance of these endangered populations. The Tiszaderzs and Lakitelek populations were sampled twice in two different years, while in the Püspökladány population, only one seed collection was performed in 2015. Samplings were performed in August, in the middle of the yielding period. Following the ENSCONET (2009) seed-collecting manual's suggestions for small populations, the aim was to collect less than 20% of the total seeds available. Depending on the size of the population, ~7–20 individuals (~50–100% of the population) were selected randomly, and 2–5 mature (brown and dried) pods were collected from them. The collected seed lots accounted for only a small proportion of the plants' total seed production as the species has continuous flowering and yielding during summer/autumn (Endrédi 2010).

Pods were opened, and only mature (round, pigmented) and intact seeds were selected for storage. In total, ~46–150 seeds were collected per population during one collection. Seeds from the same lot (collected in the same year and population) were mixed. Whereas previous observations suggested that the species is a spring germinator and a preliminary study did not show a significant effect of cold winter stratification (1 month in 4 °C) on germination (Endrédi 2010), seeds were kept in the dark, in paper bags, at room temperature (23 °C), and in ambient moisture conditions for about six months before the experiment. This time interval should be sufficient to eliminate the after-ripening period the seeds potentially need (i.e., primary dormancy) before germination.

As the size of the in-situ collected seed samples was not appropriate for repeating germination tests for years, seeds from the ex-situ population were used for the longevity experiment. For the longevity experiment, we used seeds collected from the population in four different years: 2009, 2010, 2012, and 2013 (seed lots 09EX, 10EX, 12EX, and 13EX, respectively). These ex-situ seed lots were stored under the same conditions as the in-situ seeds: in the dark, within paper bags, at room temperature (23 °C), and in ambient moist conditions.

Germination tests

Two series of germination experiments were conducted in greenhouse conditions to determine 1) the viability (estimated via germination capability) and physical dormancy of half-year-old seeds and 2) the average seed longevity (i.e., the time until the seeds can preserve their germination capacity). Experimental setups are shown in Fig. 2a. and Table 1.

Before the experiments, the average seed mass of all seed lots was estimated by weighing three subsamples containing exactly 20–20 seeds. In the case of Lakitelek seed lots (14L and 17L) we did not have 3×20 seeds; thus, we weighed all the 46–50 seeds individually to get the average seed masses. Subsamples were measured in grams with an accuracy of 0.0001 g.

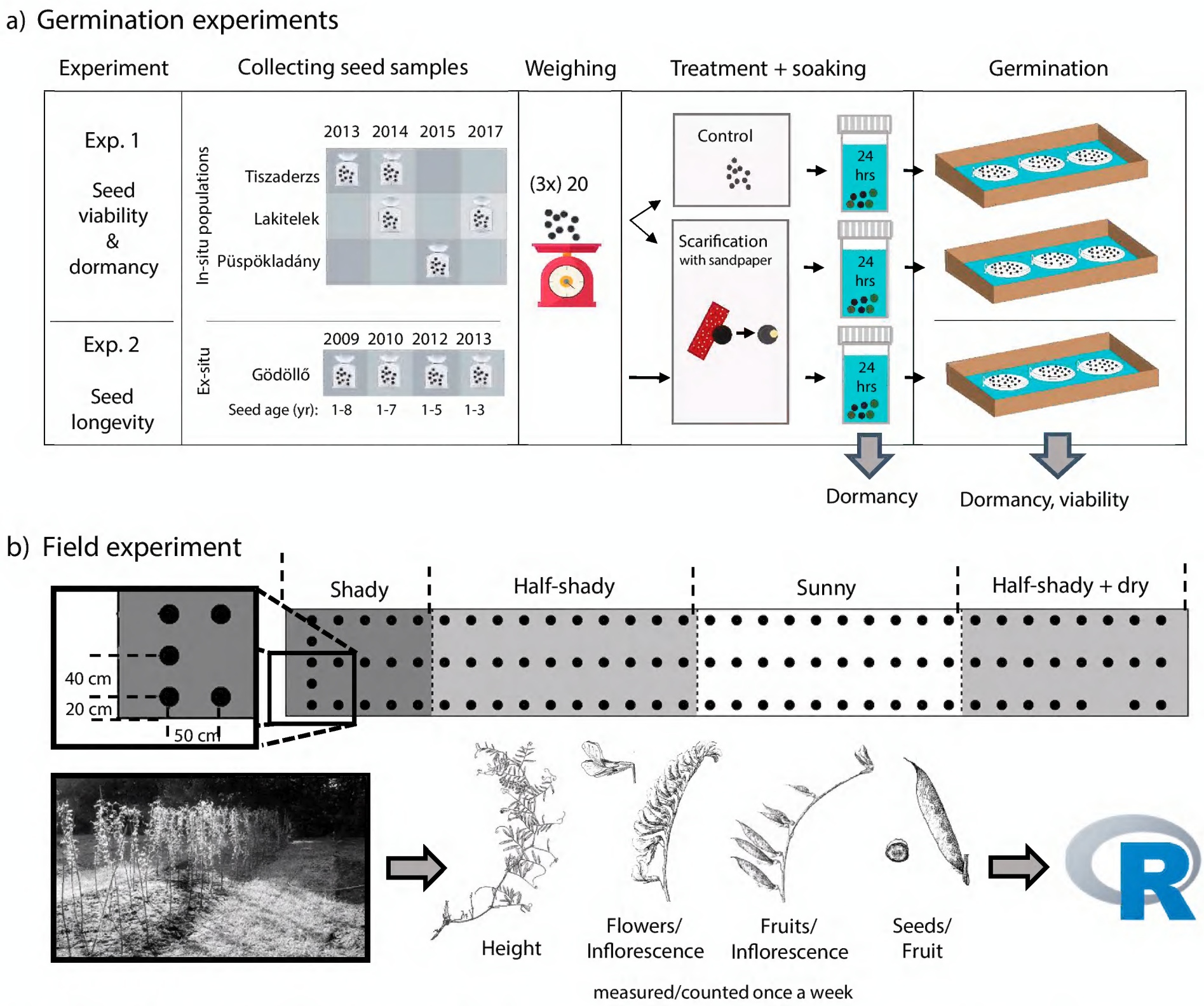

Figure 2. Materials and experimental setups of **a** the germination tests and **b** the botanical garden experiment.

Experiment 1 – Viability and dormancy tests

In the first experiment, we tested the viability and dormancy of the in-situ collected seeds, mainly focusing on physical dormancy (PY).

From the largest seed lot (15P), 120 seeds were randomly selected for the experiment, while only 80–80 seeds were available from the Tiszaderzs seed lots (13T and 14T), and all the 46–50 seeds of the Lakitelek seed lot (14L and 17L) were used in the experiment (Table 1). Before the germination test, half of the seeds in each sample were scarified individually (i.e., the seed coat was perforated) by sandpaper to break the possible physical dormancy (i.e., water-impermeable layer in the seed coat). The other half of the sample was treated as unscarified control. All (control and scarified) seeds were soaked for 24 hours in tap water. From each treatment group, at least 20 seeds (23 for 14L and 25 for 17L) were germinated in Petri dishes, with 1–3 replicates, depending on the number of available seeds (see details in Table 1).

We recorded the number of imbibed seeds daily to study the degree of physical dormancy. Physically dormant seeds could not intake water; thus, their appearance (size and colour) did not change, while seeds with broken hard

seed coats visibly swollen and their colour faded. Based on this, the physical dormancy of the seed lots was estimated as follows:

$$PY_i = 1 - ND_i = 1 - \frac{IMB_C}{IMB_C + UN_C}$$

PY*i*= level of physical dormancy in population i
ND*i*= ratio of non-dormant seeds in population i
IMB*c*= number of imbibed seeds in the control group
UN*c*= number or unchanged seeds in the control group

Table 1. Origin, treatments and number of seeds used in germination experiments. Note that seed age is rounded up as the seeds were collected in summer and germinated in spring.

Experiment	Year of collection	Source population	Seed sample	Seed age (yr)	Treatment	Sample size (n)
I. (viability & dormancy)	2013	Tiszaderzs	13T	1	Control	2*20
					Scarified	2*20
	2014	Tiszaderzs	14T	1	Control	2*20
					Scarified	2*20
		Lakitelek	14L	1	Control	23
					Scarified	23
	2015	Püspökladány	15P	1	Control	3*20
					Scarified	3*20
	2017	Lakitelek	17L	1	Control	25
					Scarified	25
II. (longevity)	2009	Gödöllő (EX)	09EX	1	Scarified	3*20
				2		3*22
				3		3*22
				7		3*20
				8		3*20
	2010	Gödöllő (EX)	10EX	1	Scarified	3*22
				2		3*22
				6		3*20
				7		3*20
	2012	Gödöllő (EX)	12EX	1	Scarified	3*20
				4		3*20
				5		3*20
	2013	Gödöllő (EX)	13EX	1	Scarified	3*20
				3		3*20
				4		3*20

Germination (root/shoot emergence) was monitored daily to investigate seed viability. As scarification was a reliable method to break physical dormancy (see in the Results section), the viability of the in-situ collected seed lots was estimated based on the germination of the scarified, imbibed seeds as physical dormancy did not prevent the germination of viable seeds in this group. However, the possible occurrence of viable seeds with combinational dormancy (PY+PD) "hiding" among the non-germinated, imbibed seeds was also considered in interpreting the results. Thus, seed viability of the in-situ collected seed lots was calculated as:

$$SV_i = \frac{GERM_{SC}}{GERM_{SC} + NG_{SC}}$$

SV_i= seed viability in population i
$GERM_{SC}$= number of germinated seeds in the scarified group
$NG_{SC=}$ number of non-germinated seeds in the scarified group

Experiment 2 – Longevity tests

In the second experiment series between 2009 and 2018, four ex-situ collected seed lots (09EX, 10EX, 12EX, and 13EX) were sampled and germinated repeatedly for 3–8 years to record the temporal dynamics of their germination capability (Table 1). Before the experiments, all seeds were scarified and soaked in tap water for 24 hours to break physical dormancy.

All germination experiments were performed in a greenhouse from the beginning of March when the temperature in the greenhouse varied between 10 °C and 20 °C. All seeds were placed onto wet filter papers in Petri dishes, and irrigation was automatic by diffusion with the help of 2cm × 20cm filter paper stripes. Imbibition and root/shoot emergence were monitored daily for 30 days.

Botanical garden experiment

Survival, development, and reproduction success were studied in 2009 in the newly established ex-situ population (Fig. 2b).

For establishing the ex-situ population, seeds of Tiszaderzs population were collected in 2007 and germinated in March 2009. In June, the well-developed (longer than 30 cm) specimens were planted on a 15 × 2m plot with sandy, fertilized, and homogeneously mixed soil and naturally diverse light conditions (Endrédi 2012; Fig. 2b). Ninety-eight individuals were planted in 3 rows and 33 columns. In the same column, individuals grew under the same light conditions, and the columns followed a natural light gradient regarding the time spent in direct sunlight (see Fig. 2b). To decrease root competition, plants were placed at least 40cm from each other: the distance between the rows was 80cm, while between the columns it was 50cm (see Fig. 2b). To estimate the plants' sensitivity to root competition, marginal specimens were planted only 20cm from the grassy edge of the seedbed.

Before planting, we classified the columns according to their light conditions (Fig. 2b): 1) shaded microsites (columns 1–5, called "Shady"), which were never exposed to direct sunlight due to a large shading tree, 2) sunny microsites (columns 16–26, called "Sunny") which were exposed to direct sunlight the whole day, and 3–4) two half-shaded microsites (columns 6–15 & columns 26–33, called "HS" and "HS + dry, respectively) with at least some hours of direct sunlight and shade every day. As the Tiszaderzs population (i.e., the source population) grew in half-shady conditions (Endrédi 2010), we used the same condition to test the species' sensitivity to precipitation. For this purpose, the two half-shady microsites were irrigated differently: while the first three microsites (Shady, Sunny, and HS) were irrigated once a week for an hour, the last half-shady microsite (HS + dry) got irrigation only every second week. This experimental setup enabled us to study plant survival, development, and reproduction success in different microsites, reflecting a wide range of light conditions and two different precipitation scenarios occurring in the different in-situ populations. We randomly distributed the specimens that germinated on the same day between the four microsites and randomly selected a column for them within the microsites to minimize the effect of germination time.

Measurements: We measured the length of the stems weekly. The number of inflorescences per individual, flowers per inflorescence, green pods per inflorescence, seeds per green pods, and the number of mature legumes were counted weekly, too. Mature pods were collected, and seeds were counted as well.

As flowering and seed production is continuous during the summer, note that with monitoring once a week, particular flowers could be counted more than once, and we could not collect all of the mature legumes before the escape of some seeds. Consequently, we cannot estimate the exact number of produced flowers or seeds, but the standard sampling makes it possible to compare the seed production of the individuals grown under different conditions.

Data processing and software

Data visualization and statistics were performed using R statistical software (R Core Team, 2019). Figures were drawn by the 'ggpubr' (Kassambara 2019) package, except Fig. 1 and Fig. 2. Fig. 1 was made with the help of 'maps' and 'mapdata' (Brownrigg et al. 2018) packages, while the river shape file is from (Tapiquén 2015), and Fig. 2 was drawn in Inkscape (Bah 2010).

Germination capabilities and dormancy of seeds in the different seed samples, as well as the effect of seed weights on seed germination probability, were compared by logistic regressions (*glm* function; R Core Team 2019), while linear model (*lm* function; R Core Team 2019) was used to compare the average seed weights of in-situ seed samples.

Regarding the garden experiment, the probability of mortality after the plantation was analysed within 6-week periods (i.e., the probability of survival in the first six weeks, between 6–12 weeks, 12–18 weeks, and 18–24 weeks after plantation). The effect of microsites (i.e., light and precipitation conditions) and root competition (marginal/inner individuals) on this probability was analysed by logistic regression. The maximum heights of plants growing in different microsites and within different root competition conditions were compared with linear models. Post hoc pairwise comparisons were made using the *glht* function of the 'multcomp' package, which automatically gives adjusted p-values (Hothorn et al. 2008). The impact of microsites and root competition (i.e., marginal or inner position) on the number of legumes and seeds was examined using the microsites/root competition in the non-parametric Kruskal-Wallis test, and pairwise Wilcoxon-test was used for posthoc pairwise comparisons.

Results

Germination tests

Experiment 1 – Viability and dormancy tests

The results of the first experiment are summarized in Fig. 3.

Generally, the seeds of the species showed high viability (on average, 78–88% of the scarified seeds germinated), and there were no significant differences between the different in-situ seed lots (adjusted $p>0.08$, logistic regression) (Fig. 3a). Furthermore, the level of physical dormancy was also high in every seed lot (adjusted $p>0.88$, logistic regression): only 0–10% of the control seeds showed visually noticeable water uptake (Fig. 3b), indicating the absence of water-imperme-

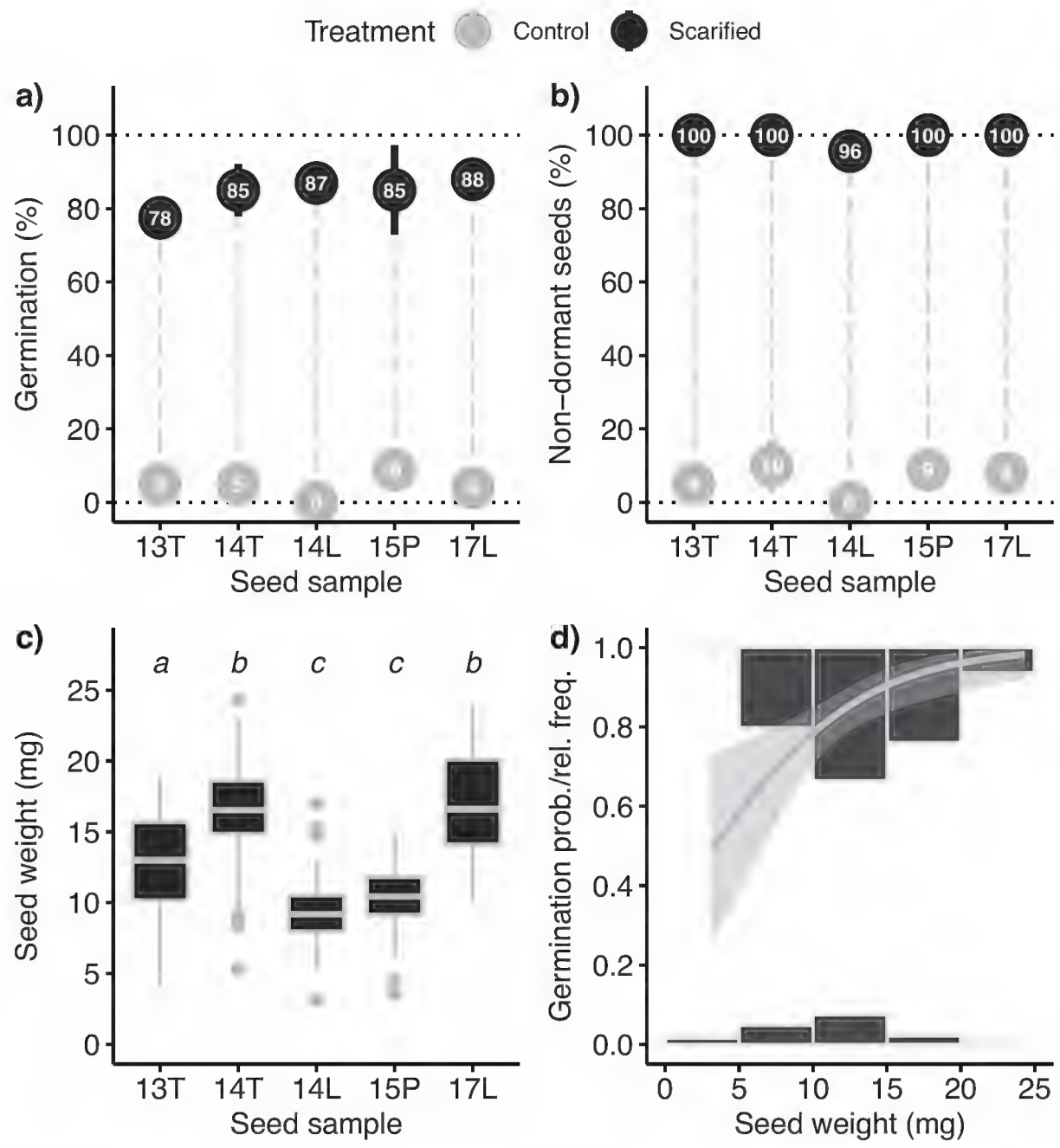

Figure 3. Results of the first germination experiment: seed viability (**a**), dormancy (**a, b**), seed weight (**c**) and their relationship (germination probability/relative frequency of scarified seeds with different weights) (**d**) in the case of half-year-old, in-situ collected seeds. Different characters in panel c indicate significantly different seed lots (linear model, Tukey's contrasts). In panel **d**, the heights of the bars represent the relative frequencies of germinated (hanging bars) and non-germinated (standing bars) seeds in the different seed weight classes. The sum of the heights of all bars is equal to one. E.g., 4.78% of the examined scarified seeds weighed between 5-10 mg and showed no germination (second standing bar), while another 20.21% of all tested seeds fell into the same weight category but did germinate in the experiment (second hanging bar). The fitted line shows the relationship between the seed weight and the germination capability, predicted by the logistic regression model.

able seed coat (i.e., the absence of physical dormancy). Individual scarification proved to be a suitable method for breaking this high level of physical dormancy – 96–100% of the seeds could take up water after the treatment (Fig. 3b), with a significant 72–87% increase in germination capability as well (Fig. 3a).

Almost all seed samples were different in average seed mass ($p<0.001$, linear model) (Fig. 3c), even the ones that came from the same population but different years (13T/14T and 14L/17L pairs), and those collected in the same year but from different populations (14T/14L). However, heavier seeds had a higher germination probability ($p<0.01$, logistic regression), germination probability of seeds with more than 10 mg mass was found to be high, exceeding 0.8 (Fig. 3d).

Experiment 2 – Longevity tests

The results of the second experiment series are shown in Fig. 4.

Despite the highly protective seed coat (i.e., the generally high initial physical dormancy) and high initial viability, all examined ex-situ collected seed samples

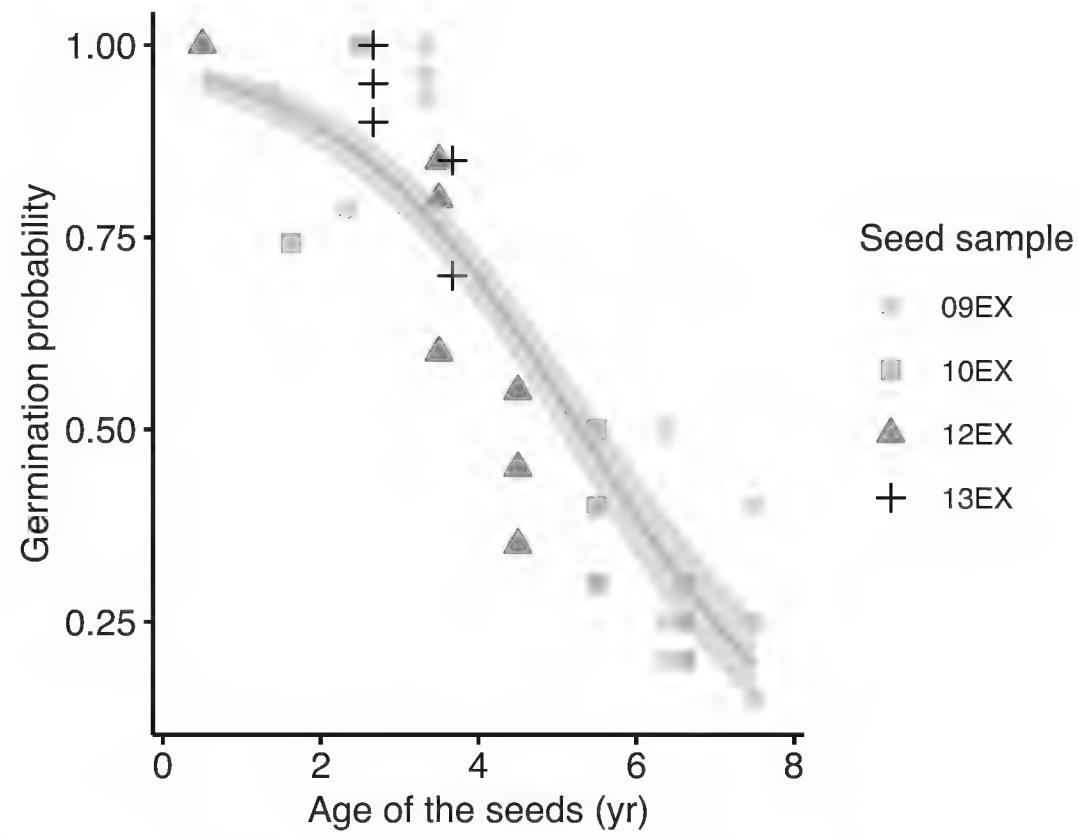

Figure 4. Temporal changes in seed viability of ex-situ collected seeds.

showed a sharp decrease in germination capability in the first 5–6 years ($p<0.001$, logistic regression) (Fig. 4). The logistic regression model suggests that germination capability probably decreases below 10% within ten years when these seeds are stored at room temperature and ambient relative humidity.

Botanical garden experiment

Summary statistics (mean and SD) of traits (lifespan, height, pod, and seed production) measured on the different microsites are summarized in Table 2.

Table 2. Summary statistics (mean and sd) of the traits of plants grown in the botanical garden in different light and precipitation conditions (Shady= always shaded weekly irrigated microsite (n=17), HS= half-shaded, weekly irrigated microsite (n=30), Sunny= always sunny, weekly irrigated microsite (n=30), HS+dry= half-shaded, biweekly irrigated microsite (n=23)).

Microsite	Lifespan (weeks)		Max. height (cm)		Number of pods/ individual		Number of seeds/ individual		Number of seeds/ pods	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
Shady	21.00	3.78	201.37	41.42	80.43	39.79	264.43	111.56	3.39	0.63
HS	18.33	5.96	276.91	50.82	148.07	76.67	529.25	256.75	3.62	0.40
Sunny	15.30	8.82	209.00	54.43	184.50	130.95	679.91	507.77	3.69	0.36
HS + dry	14.39	5.98	161.47	49.52	53.45	51.44	183.05	152.20	3.67	0.49

Survival and development

All ex-situ planted individuals (n=98) germinated, established and finished their life cycle within one vegetation season (from spring to autumn) as summer annual plants. Within the 24-week-long field experiment, the highest average lifespan (21 weeks after plantation) was found in shady conditions, and a decreasing trend was observed along the light gradient (Half-shady (HS)=18.3 weeks, and Sunny=15.3 weeks, Fig. 5a). However, individuals growing on the drier half-shady part (HS + dry) of the plot showed the lowest average lifespan (14.4 weeks).

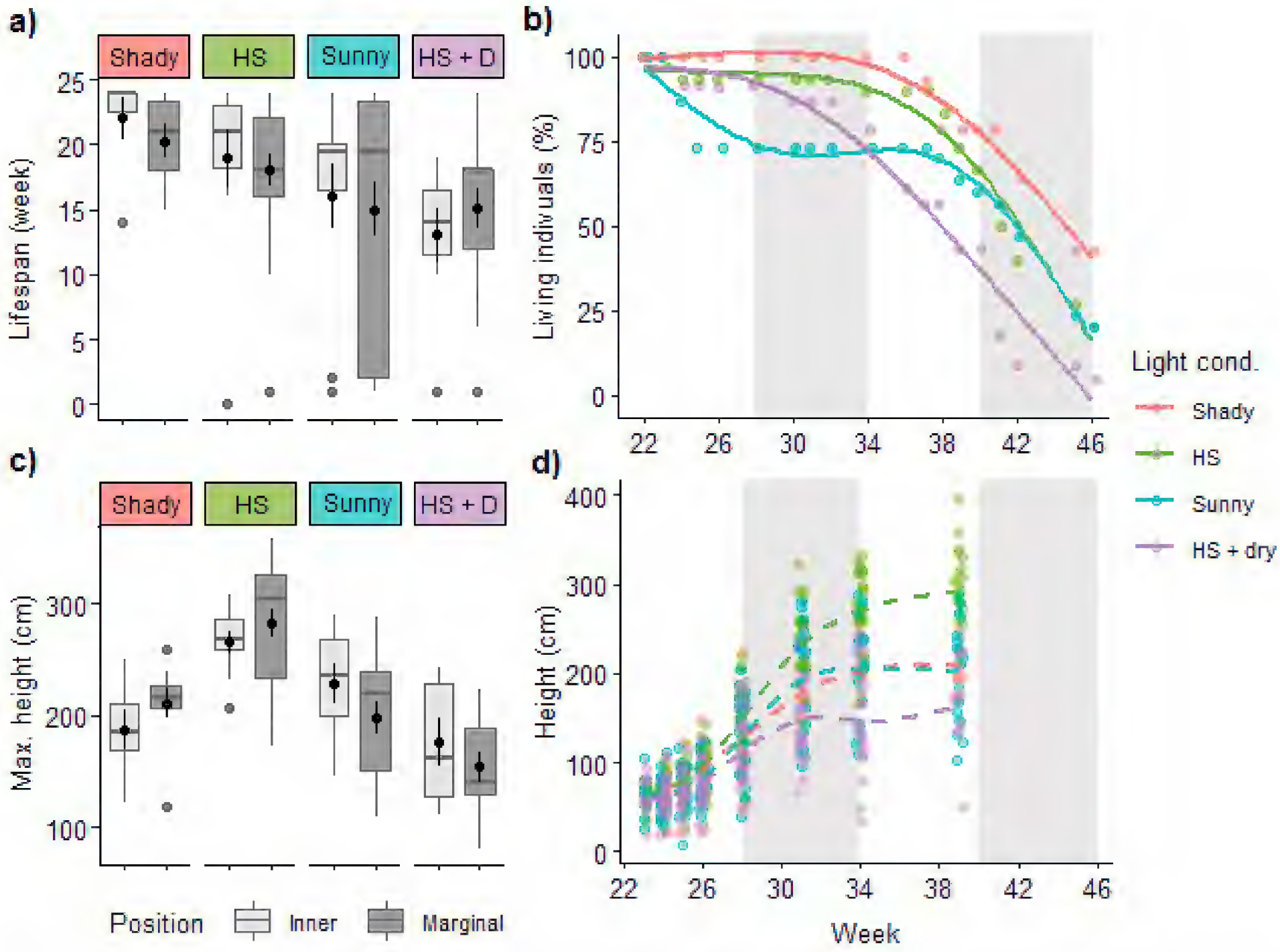

Figure 5. Survival and growing in different light conditions and competition: lifespan after plantation (mean + SE) (**a**), temporal patterns in survival (**b**), maximum height (mean + SE) (**c**) and temporal patterns in growing (**d**). Lighter boxplots show individuals with no competitors within 40cm, while darker boxplots indicate plants with neighbouring grass in 20cm distance. Dots and bars on the boxplots show mean and SE values. Grey and white stripes on panels **b** and **d** indicate 6-week-long periods.

Plants grown in the marginal position showed a slightly, but not significantly lower average lifespan than their neighbours in the middle of the plot. The temporal change in mortality is presented in Fig. 5b. Plants growing under direct sunlight were found to be more vulnerable to the stress caused by planting, as 26.7% of the individuals died in the first few weeks after planting. In contrast, in half-shady areas, the mortality rate was 18–20% less, while in the shade, none of the individuals died within the first six weeks. In general, the mortality rate started to increase 12 weeks after plantation (from week 34, middle of August, after the plants reached their maximum height (Fig. 5d)), but plants growing under different light conditions showed different patterns: on the drier half-shady part of the plot, the increase started some weeks earlier than on the shady or sunny parts.

The plants reached their maximum height 12–16 weeks after plantation (Fig. 5d), and it was significantly the highest (mean=276.9 cm, sd=50.8) in the half-shady, weekly irrigated microsite (HS), while the smallest plants (with an average of 161.5 cm and sd=49.5) were found on the half-shady, but rarely irrigated microsite (HS + dry) (Table 2). There was no difference between the maximum height of plants growing in shady (mean=201.4 cm, sd=41.4) and sunny (mean=209.0 cm, sd=54.4) conditions, but both groups differed significantly from the half-shady groups ($p<0.03$, linear regression). There was no significant

difference in the maximum stem length of plants growing at the edge/middle of the plot as well (i.e., in different root competition conditions, Fig. 5c).

Reproduction

Flowering started around week 28, reached the peak around week 33, and ended around week 39 (Fig. 6b). However, the timing of flowering seems to be independent of the light and competition conditions (Fig. 6a, b), the number of flowers per individuals showed some differences (Fig. 6b): plants which were grown in the half-shady and weekly irrigated microsite (HS) had more flowers than those in the other groups.

The first pods appeared two weeks after the start of flowering. The number of pods showed a similar temporal pattern to the flower's (Fig. 6d), with the highest values in the half-shady, weekly irrigated area (HS), but the average total number of matured pods per individual (Fig. 6c) was similarly high in the sunny area too ($p=0.61$, pairwise Wilcoxon test). All the other group pairs differed significantly ($p<0.04$, pairwise Wilcoxon test). As the number of seeds in the pods was independent of the conditions (Table 2), the total number of seeds showed

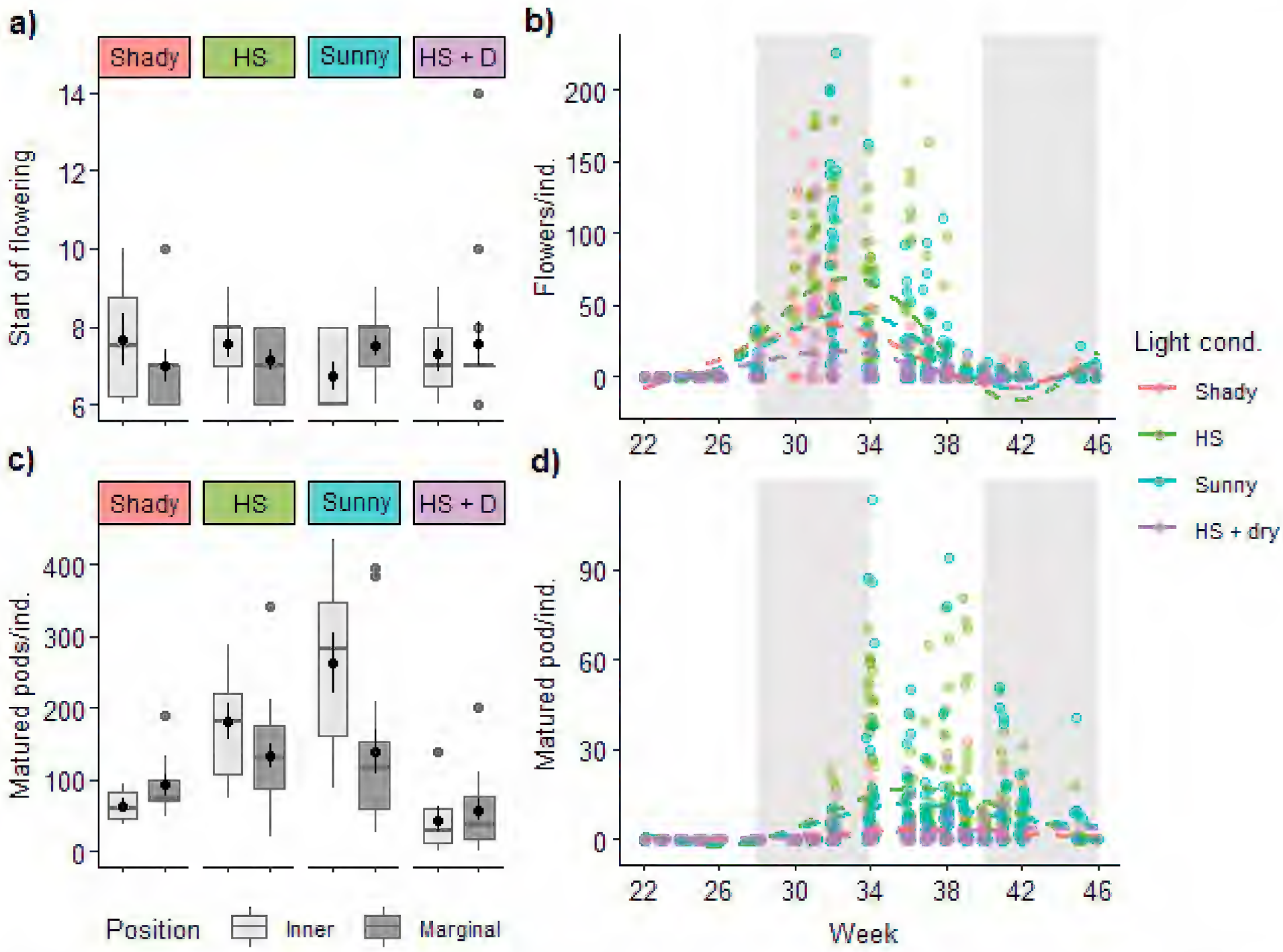

Figure 6. Flowering and yielding in different light conditions and competition: first week of flowering after plantation (**a**), temporal patterns in flowering (**b**), number of matured pods/individual (**c**) and temporal patterns in producing pods (**d**). Lighter boxplots show individuals with no competitors within 40cm, while darker boxplots indicate plants with neighbours within 20cm distance. Dots and bars on the boxplots show mean and SE values. Grey and white stripes on panels **b**) and **d**) indicate 6-week-long periods.

a similar pattern as the pods: the plants produced the lowest number of seeds in the half-shady, dry (HS + dry) area (mean=183.05, sd=152.2), slightly more in shady conditions (Shady, mean=264.4, sd=111.6), while the best performance was observed on the weekly irrigated half-shady (HS, mean=529.3, sd=256.8) and sunny (mean=679.9, sd=507.8) microsites (Table 2). Regarding the edge effect, only the sunny group showed a significant difference; plants grown in the middle of the plot, far from each other, produced more pods and seeds than their neighbours on the edge of the plot, where the root competition with grasses was more emphasized (p=0.029, Wilcoxon test).

Discussion

To summarize our results, *Vicia biennis* seeds showed high seed viability and physical dormancy in all the studied Hungarian populations, while seed mass was highly variable across years and source populations. The germination results suggest that the species has a long-term persistent seed bank, but seed viability sharply decreases below 10% within ten years in dry storage and room temperature.

All specimens in our experiment behaved as annual (not biennial), and their mortality, growth, and reproduction showed a strong sensitivity for irrigation/soil moisture content: on sandy but fertilized soil and in half-shady conditions, the plants performed significantly better (lived longer, grew higher and produced more flowers and seeds) when they were irrigated weekly and not only every second week. When getting the same amount of water, the plants had longer stems and more flowers in the half-shady area than in shady or sunny conditions, but the pod and seed production were similar or even higher (when competition for water was low) on the sunny part of the plot. However, higher competition for the limited water resulted in a significant decrease in seed production.

Annual plant species are typically associated with highly disturbed and temporally variable habitats, where producing seeds with different dormancy levels and high longevity can efficiently “spread the risk” caused by the unpredictable environment (Cohen 1966; Childs et al. 2010). Seed dormancy is a widespread, adaptive strategy for avoiding unfavourable conditions in a seasonally variable environment (Westoby 1981; Rubio de Casas et al. 2017). In theory, seed dormancy is generally more important for annuals as the vegetative phase of their life is short, and a massive part of their populations exist only in seed banks (Cohen 1966; Pake and Venable 1996; Childs et al. 2010). However, even in the case of annuals, high dormancy is rather expected in highly unpredictable, stochastic environments (Venable and Brown 1988; Philippi 1993; Volis and Bohrer 2013). Furthermore, environmental factors (i.e., mainly annual precipitation) in the year of seed production can also modify the ratio of dormant seeds produced, especially in habitats with poor water supply (Cseresnyés-Bózsing 2010).

V. biennis is mainly connected to the edge of temporal or persistent wetland habitats, and we found that the adult plants show a strong sensitivity to water availability. Based on this, a possible explanation for the generally observed high seed dormancy across populations and years can be the widespread insufficient precipitation or high inter-annual variation in precipitation in their habitats. The long-term climate data of Hungary support this: in the last decades, there was a significant decrease in spring precipitation and the number of wet days (with more than 1mm rainfall), and an increasing trend in the duration of dry seasons,

while a large inter-annual variation can be observed for all the three parameters (Lakatos et al. 2018). On the other hand, high dormancy can also result from the strong competition for water (Harel et al. 2011). Evidence suggests that in some cases, mostly in disturbed areas, *V. biennis* can appear further away from water bodies, while in the Tiszaderzs and Lakitelek populations, it has disappeared from areas where the vegetation cover had increased. In addition, our botanical garden experiment showed that in a sunny area, where the higher evaporation rate can lead to lower soil moisture, increased root competition significantly negatively affected seed production. Based on these, the adult plants seem sensitive to insufficient water supply and have low competitiveness for water. Thus, consistently high physical dormancy can indicate temporally suboptimal conditions in all examined populations (i.e., increasing aridity or competition), or it may be a sign that the species or its local populations are adapted to a highly unpredictable, stochastic environment (Cohen 1966; Childs et al. 2010).

Seed mass is also important in coping with environmental stress. At an individual level, larger seeds support a higher survival rate for seedlings (Westoby et al. 2002) and adult plants (Metz et al. 2010) and can increase the longevity of the seeds (by the greater storage capacity), especially when combined with a hard seed coat (which effectively protects the embryo) (Debeaujon et al. 2007). However, the larger predation pressure on these seeds can limit the seed mass in a population (Volis and Bohrer 2013), and as there is a trade-off between seed size and seed number, seed size depends more on the local environment of the mother plant too (Debeaujon et al. 2007). For example, many studies found that plants produce larger seeds in shaded habitats than in more open areas (e.g., Salisbury 1942; Hodkinson et al. 1998; Sonkoly et al. 2017).

In this study, we found significant differences in the seed weights between the different populations and years. In general, we found significantly larger seeds in the larger populations (Tiszaderzs and Lakitelek in 2017) containing more than 20 individuals, while the 10–15 individuals living in the smallest populations (Püspökladány and Lakitelek in 2014) produced the smallest seeds. Although seed mass usually correlates with seed viability (i.e., seeds developed in unfavourable conditions are often less viable), we found high seed viability in all populations. A possible explanation for this is that even these populations with small seeds have reached an average seed weight of 10 mg, which – according to our logistic model – can be enough to maintain high seed viability (i.e., an expected germination capacity higher than 0.8). These results suggest that the small numbers of individuals in the populations have not yet led to a significant deterioration in seed quality.

At the species level, seed longevity shows some correlation with other seed traits, like seed mass: species with smaller average seed mass are more likely to have long-term persistent seed banks (i.e., seeds that are still viable after five years in the seed bank) (Thompson et al. 1993; Hodkinson et al. 1998; Csontos 2001). According to the 8-grade seed weight category system of Csontos (2001), *V. biennis* has relatively large seeds belonging to the 7th group (i.e., species with average seed weight between 10.1 and 50 mg). Based on this, a transient seed bank (with seeds that are viable for less than a year after dispersal) would be expected, but according to Thompson et al. (1998), the majority of variance in seed persistence cannot be explained by seed mass, because seed longevity is more a species attribute, and more dependent of phylogeny and life history of the species than seed mass. Most *Vicia* species living in the same region have

similar average seed weights as *V. biennis*, and many have persistent seed banks (Csontos 2001; Kleyer et al. 2008). However, data about seed bank types of *Vicia* species are scarce and sometimes contradictory. On the other hand, shorter life histories correlate with increased seed longevity and habitat specialists of disturbed habitat types (often annuals) show higher persistence in soils than those of stable, undisturbed habitats (Thompson et al. 1998). These findings support our results that *V. biennis* is more likely to have a long-term persistent seed bank, and its seeds can preserve their germination capability for more than five years. Although we experienced a sharp decrease in germination after five years of dry storage at room temperature, our results do not necessarily reflect the true (ex-situ or in-situ) seed longevity. In their natural environment (i.e., in lower temperatures of the natural seed bank), seeds can remain viable for a longer time than in our experiment, and the realized persistence in the soil also depends on other factors (i.e., soil moisture, depth, temperature fluctuations, seed predation, microorganism). Based on the LEDA database, no *Vicia* species has yet been found with a seed life expectancy exceeding 25 years (Kleyer et al. 2008), so we do not expect *V. biennis* to have higher seed longevity, but for a more precise determination, appropriate experiments, either in-situ or ex-situ, are needed.

From a conservation perspective, the most crucial question is how threatened the species actually is by climate change or habitat change/loss. According to the climate models of Hungary (Lakatos et al. 2018), due to the decreasing annual precipitation and increasing mean annual temperature, the soil moisture content is expected to decrease, and the frequency and duration of droughts will increase in the future. The rainfall deficit will affect the summers the most when *V. biennis* is most sensitive to adequate soil moisture and lower competition for water during flowering. This makes it increasingly unlikely that stable populations will be established further away from wetlands. However, wetlands are not only becoming increasingly threatened globally but are also changing locally. With increasingly rare periods of extreme rainfall events, regulated shorelines and reduced grazing, the competition-poor environment required by the species is becoming less and less likely.

The species' long-term survival will depend on how it can adapt to these changes or 'escape' them and find more suitable areas.

Adaptive capacity is based on the adequate genetic diversity of populations. In small, highly fluctuating populations, genetic diversity is more likely to be reduced by inbreeding and genetic drift, and these populations may become more sensitive to environmental change (Bouzat 2010).

The probability and level of inbreeding depression depend on the species' mating system. Although self-compatibility of flowers is common in the Fabaceae family (e.g., Zhang and Mosjidis 1995), we do not have information about the possibility or frequency of self-pollination in the case of *V. biennis*. It also needs to be discovered how isolated the populations of the species actually are. Regarding pollinators, only common *Bombus* species have been observed as active pollinators to date (A. E. personal observation). The estimated foraging distance of these species does not exceed 1000m (Cresswell et al. 2000), so they are not suitable for maintaining gene flow between the natural populations of the plant. However, the contribution of other pollinator species cannot be excluded.

The primary mechanism to escape from the negative effects of climate and habitat change is dispersal. Similarly to other *Vicia* species (e.g., Oleas et al.

2018), in the case of *V. biennis*, short-distance dispersal (for a few meters) is achieved by the explosive opening of mature fruits and the ejection of seeds (called "ballochory") (A. E., personal observation), but other mechanisms of dispersal are unknown. However, maintaining a large, persistent and highly dormant soil seed bank may be an appropriate strategy to avoid unfavourable conditions, not in space but in time. However, this strategy is only successful if conditions in the habitat become optimal at specific intervals.

Marini et al. (2012) suggest that the three most important traits that can help cope with the effects of habitat loss and isolation are annual life form (i.e., short generation time usually coupled with large persistent seed banks), high competitive ability and animal dispersal (i.e., non-random long-distance dispersal helping to reach suitable habitats). Although *V. biennis* is probably an annual plant with reproductive traits well adapted to unpredictable environments, its competitive ability – especially for water – is low, and there is no reliable data about animal dispersal. Based on this, the species' sensitivity to further habitat loss or isolation can be high, and if the frequency of wet years or the disturbance events in suitable wetlands decreases under a threshold, seed banks can be depleted, and these small western marginal populations can disappear.

Based on the above, the following conservation priorities are suggested:

1. To assess the actual vulnerability of the species, it is essential to assess the populations' current genetic diversity and isolation. This should be complemented by an investigation of the state of the soil seed bank and appropriate experimental studies of seed longevity.
2. In-situ conservation actions should primarily target the vegetation of the habitat and the seed bank of the species: continuous, controlled disturbance of the sites and reinforcement of the seed bank by seed sowing can help the species to persist in a given area. In the long-term, assisted migration may also be an option, where seed sowing is used to help the species spread to new areas likely to provide suitable conditions in the longer term.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The work of BD was supported by the NKFI FK 135329 project, while the work of OV was supported by the NKFI KKP 144096 project.

Author contributions

AE and JGYN designed the experiments and collected the seed material. AE, ÁS, and DÉ did the germination experiments, AE conducted the botanical garden experiment, analyzed the data, and wrote the first version of the manuscript. JGYN, BD, and OV contributed to the final version of the manuscript.

Author ORCIDs

Anett Endrédi https://orcid.org/0000-0001-6572-6468
Ármin Sőth https://orcid.org/0000-0002-6417-3168
Balázs Deák https://orcid.org/0000-0001-6938-1997
Orsolya Valkó https://orcid.org/0000-0001-7919-6293
János György Nagy https://orcid.org/0009-0005-3854-0840

Data availability

All of the data that support the findings of this study are available in the main text.

References

Anon (2020) Royal Botanic Gardens Kew. Seed Information Database (SID).

Bah T (2010) Inkscape - Guide to a vector drawing program. 3rd edn. Ann Arbor, Michigan, 38 pp. http://tavmjong.free.fr/INKSCAPE/

Bartha D, Bán M, Schmidt D, Tiborcz V (2023) Vascular plants of Hungary online database. Department of Botany and Nature Conservation, Faculty of Forestry, Sopron University. http://floraatlasz.uni-sopron.hu

Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography, and, evolution of dormancy and germination. Academic Press, San Diego, California, USA, 666 pp.

Baskin JM, Baskin CC (2004) A classification system for seed dormancy. Seed Science Research 14(1): 1–16. https://doi.org/10.1079/SSR2003150

Bekker RM, Bakker JP, Grandin U, Kalamees R, Milberg P, Poschlod P, Thompson K, Willems JH (1998) Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. Functional Ecology 12(5): 834–842. https://doi.org/10.1046/j.1365-2435.1998.00252.x

Bekker RM, Bakker JP, Ozinga WA, Thompson K (2003) Seed traits: Essential for understanding seed longevity. Aspects of Applied Biology 69: 1–9.

Borhidi A (1995) Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora. Acta Botanica Hungarica 39: 97–181.

Botta-Dukát Z, Bartha D, Dancza I, Lukács BA, Pinke G (2023) Adaptation of life form categorisation of Ellenberg and Mueller-Dombois to the Hungarian Flora. Acta Botanica Hungarica 65(1–2): 1–34. https://doi.org/10.1556/034.65.2023.1-2.1

Bouzat JL (2010) Conservation genetics of population bottlenecks: The role of chance, selection, and history. Conservation Genetics 11(2): 463–478. https://doi.org/10.1007/s10592-010-0049-0

Brownrigg R, Minka PT, Deckmyn A (2018) maps: Draw Geographical Maps. https://cran.r-project.org/package=maps

Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. Proceedings of the Royal Society B, Biological Sciences 277(1697): 3055–3064. https://doi.org/10.1098/rspb.2010.0707

Cohen D (1966) Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology 12(1): 119–129. https://doi.org/10.1016/0022-5193(66)90188-3

Cresswell JE, Osborne JL, Goulson D (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecological Entomology 25(3): 249–255. https://doi.org/10.1046/j.1365-2311.2000.00264.x

Cseresnyés-Bózsing E (2010) A hólyagos csüdfű (*Astragalus cicer* L.) magprodukciójának és csírázóképességének vizsgálata. Botanikai Közlemények 97: 49–57.

Csontos P (2001) A természetes magbank kutatásának módszerei. Scientia, Budapest, 155 pp.

Csontos P, Kalapos T, Tamás J (2016) Comparison of seed longevity for thirty forest, grassland and weed species of the central European flora: Results of a seed burial experiment. Polish Journal of Ecology 64(3): 313–326. https://doi.org/10.3161/15052249PJE2016.64.3.002

Debeaujon I, Lepiniec L, Pourcel L, Routaboul J-M (2007) Seed coat development and dormancy. In: Bradford KJ, Nonogaki H (Eds) Annual Plant Reviews - Seed dormancy and germination. Blackwell Publishing, 25–41. https://doi.org/10.1002/9780470988848.ch2

Dee LE, Cowles J, Isbell F, Pau S, Gaines SD, Reich PB (2019) When Do Ecosystem Services Depend on Rare Species? Trends in Ecology & Evolution 34(8): 746–758. https://doi.org/10.1016/j.tree.2019.03.010

Endrédi A (2010) A kunsági bükköny (*Vicia biennis* L.) ex-situ szaporítása. BSc Thesis, Szent István University, Gödöllő, Hungary.

Endrédi A (2012) Védett növények ex-situ védelme. MSc Thesis, Szent István University, Gödöllő, Hungary.

Endrédi A, Nagy JG (2012) Adatok a fokozottan védett kunsági bükköny (*Vicia biennis* L.) élőhely-preferenciájáról. [Data about the habitat preferences of *Vicia biennis* L.]. Kitaibelia 17: 21. http://real-j.mtak.hu/16313/1/2012_17_1.pdf

Enquist BJ, Feng X, Boyle B, Maitner B, Newman EA, Jørgensen PM, Roehrdanz PR, Thiers BM, Burger JR, Corlett RT, Couvreur TLP, Dauby G, Donoghue JC, Foden W, Lovett JC, Marquet PA, Merow C, Midgley G, Morueta-Holme N, Neves DM, Oliveira-Filho AT, Kraft NJB, Park DS, Peet RK, Pillet M, Serra-Diaz JM, Sandel B, Schildhauer M, Šímová I, Violle C, Wieringa JJ, Wiser SK, Hannah L, Svenning JC, McGill BJ (2019) The commonness of rarity: Global and future distribution of rarity across land plants. Science Advances 5(11): 1–14. https://doi.org/10.1126/sciadv.aaz0414

ENSCONET (2009) Seed Collecting Manual for Wild Species, 32 pp.

Ércz D (2018) A kunsági bükköny védelme és ex-situ szaporítása. MSc Thesis, Szent István University, Gödöllő, Hungary.

Farkas S [Ed.] (1999) Magyarország védett növényei. Mezőgazda Kiadó, Budapest, Magyarország, 416 pp.

Godefroid S, Piazza C, Rossi G, Buord S, Stevens AD, Aguraiuja R, Cowell C, Weekley CW, Vogg G, Iriondo JM, Johnson I, Dixon B, Gordon D, Magnanon S, Valentin B, Bjureke K, Koopman R, Vicens M, Virevaire M, Vanderborght T (2011) How successful are plant species reintroductions? Biological Conservation 144(2): 672–682. https://doi.org/10.1016/j.biocon.2010.10.003

Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. Journal of Ecology 86(6): 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Gulyás G (2013) A kunsági bükköny (*Vicia biennis* L.) előfordulása Püspökladány mellett. Kitaibelia 18: 178–186.

Harel D, Holzapfel C, Sternberg M (2011) Seed mass and dormancy of annual plant populations and communities decreases with aridity and rainfall predictability. Basic and Applied Ecology 12(8): 674–684. https://doi.org/10.1016/j.baae.2011.09.003

Házi J, Lesku B (2006) A nemzeti park igazgatóságok által ex-situ védelemre javasolt növényfajok listája. Debrecen.

Hodkinson DJ, Askew AP, Thompson K, Hodgson JG, Bakker JP, Bekker RM (1998) Ecological correlates of seed size in the British flora. Functional Ecology 12(5): 762–766. https://doi.org/10.1046/j.1365-2435.1998.00256.x

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical Journal. Biometrische Zeitschrift 50(3): 346–363. https://doi.org/10.1002/bimj.200810425

Jain M, Flynn DFB, Prager CM, Hart GM, DeVan CM, Ahrestani FS, Palmer MI, Bunker DE, Knops JMH, Jouseau CF, Naeem S (2014) The importance of rare species: A trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. Ecology and Evolution 4(1): 104–112. https://doi.org/10.1002/ece3.915

Jaureguiberry P, Titeux N, Wiemers M, Bowler DE, Coscieme L, Golden AS, Guerra CA, Jacob U, Takahashi Y, Settele J, Díaz S, Molnár Z, Purvis A (2022) The direct drivers of recent global anthropogenic biodiversity loss. Science Advances 8: 9982. https://doi.org/10.1126/sciadv.abm9982

Jayasuriya K, Wijetunga A (2013) Seed dormancy and storage behavior in tropical Fabaceae: A study of 100 species from Sri Lanka. Seed Science Research 23(4): 1–13. https://doi.org/10.1017/S0960258513000214

Jiménez-Alfaro B, Silveira FAO, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. Journal of Vegetation Science 27: 637–645. https://doi.org/10.1111/jvs.12375

Kassambara A (2019) ggpubr: 'ggplot2' Based Publication Ready Plots. https://cran.r-project.org/package=ggpubr

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Van Bodegom PM, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly DD, Anand M, Atkin O, Bahn M, Baker TR, Baldocchi D, Bekker R, Blanco CC, Blonder B, Bond WJ, Bradstock R, Bunker DE, Casanoves F, Cavender-Bares J, Chambers JQ, Chapin FS III, Chave J, Coomes D, Cornwell WK, Craine JM, Dobrin BH, Duarte L, Durka W, Elser J, Esser G, Estiarte M, Fagan WF, Fang J, Fernández-Méndez F, Fidelis A, Finegan B, Flores O, Ford H, Frank D, Freschet GT, Fyllas NM, Gallagher RV, Green WA, Gutierrez AG, Hickler T, Higgins SI, Hodgson JG, Jalili A, Jansen S, Joly CA, Kerkhoff AJ, Kirkup D, Kitajima K, Kleyer M, Klotz S, Knops JMH, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee TD, Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, Llusià J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, Müller SC, Nadrowski K, Naeem S, Niinemets Ü, Nöllert S, Nüske A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, Ordoñez J, Overbeck G, Ozinga WA, Patiño S, Paula S, Pausas JG, Peñuelas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negret B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana JF, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY - a global database of plant traits. Global Change Biology 17(9): 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, Acosta ATR, Adamidis GC, Adamson K, Aiba M, Albert CH, Alcántara JM, Alcázar C C, Aleixo I, Ali H, Amiaud B, Ammer C, Amoroso MM, Anand M, Anderson C, Anten N, Antos J, Apgaua DMG, Ashman T-L, Asmara DH, Asner GP, Aspinwall M, Atkin O, Aubin I, Baastrup-Spohr L, Bahalkeh K, Bahn M, Baker T, Baker WJ, Bakker JP, Baldocchi D, Baltzer J, Banerjee A, Baranger A, Barlow J, Barneche DR, Baruch Z, Bastianelli D, Battles J, Bauerle W, Bauters M, Bazzato E, Beckmann M, Beeckman H, Beierkuhnlein C, Bekker R, Belfry G, Belluau M, Beloiu M, Benavides R, Benomar L, Berdugo-Lattke ML, Berenguer E, Bergamin R, Bergmann J, Bergmann Carlucci M, Berner L, Bernhardt-Römermann M, Bigler C, Bjorkman AD, Blackman C, Blanco C, Blonder B, Blumenthal D, Bocanegra-González KT, Boeckx P, Bohlman S, Böhning-Gaese K, Boisvert-Marsh L, Bond W, Bond-Lamberty B, Boom A, Boonman CCF, Bordin K, Boughton EH, Boukili V, Bowman DMJS, Bravo S, Brendel MR, Broadley MR, Brown KA, Bruelheide H, Brumnich F, Bruun HH,

Bruy D, Buchanan SW, Bucher SF, Buchmann N, Buitenwerf R, Bunker DE, Bürger J, Burrascano S, Burslem DFRP, Butterfield BJ, Byun C, Marques M, Scalon MC, Caccianiga M, Cadotte M, Cailleret M, Camac J, Camarero JJ, Campany C, Campetella G, Campos JA, Cano-Arboleda L, Canullo R, Carbognani M, Carvalho F, Casanoves F, Castagneyrol B, Catford JA, Cavender-Bares J, Cerabolini BEL, Cervellini M, Chacón-Madrigal E, Chapin K, Chapin FS, Chelli S, Chen S-C, Chen A, Cherubini P, Chianucci F, Choat B, Chung K-S, Chytrý M, Ciccarelli D, Coll L, Collins CG, Conti L, Coomes D, Cornelissen JHC, Cornwell WK, Corona P, Coyea M, Craine J, Craven D, Cromsigt JPGM, Csecserits A, Cufar K, Cuntz M, da Silva AC, Dahlin KM, Dainese M, Dalke I, Dalle Fratte M, Dang-Le AT, Danihelka J, Dannoura M, Dawson S, de Beer AJ, De Frutos A, De Long JR, Dechant B, Delagrange S, Delpierre N, Derroire G, Dias AS, Diaz-Toribio MH, Dimitrakopoulos PG, Dobrowolski M, Doktor D, Dřevojan P, Dong N, Dransfield J, Dressler S, Duarte L, Ducouret E, Dullinger S, Durka W, Duursma R, Dymova O, E-Vojtkó A, Eckstein RL, Ejtehadi H, Elser J, Emilio T, Engemann K, Erfanian MB, Erfmeier A, Esquivel-Muelbert A, Esser G, Estiarte M, Domingues TF, Fagan WF, Fagúndez J, Falster DS, Fan Y, Fang J, Farris E, Fazlioglu F, Feng Y, Fernandez-Mendez F, Ferrara C, Ferreira J, Fidelis A, Finegan B, Firn J, Flowers TJ, Flynn DFB, Fontana V, Forey E, Forgiarini C, François L, Frangipani M, Frank D, Frenette-Dussault C, Freschet GT, Fry EL, Fyllas NM, Mazzochini GG, Gachet S, Gallagher R, Ganade G, Ganga F, García-Palacios P, Gargaglione V, Garnier E, Garrido JL, de Gasper AL, Gea-Izquierdo G, Gibson D, Gillison AN, Giroldo A, Glasenhardt M-C, Gleason S, Gliesch M, Goldberg E, Göldel B, Gonzalez-Akre E, Gonzalez-Andujar JL, González-Melo A, González-Robles A, Graae BJ, Granda E, Graves S, Green WA, Gregor T, Gross N, Guerin GR, Günther A, Gutiérrez AG, Haddock L, Haines A, Hall J, Hambuckers A, Han W, Harrison SP, Hattingh W, Hawes JE, He T, He P, Heberling JM, Helm A, Hempel S, Hentschel J, Hérault B, Hereş A-M, Herz K, Heuertz M, Hickler T, Hietz P, Higuchi P, Hipp AL, Hirons A, Hock M, Hogan JA, Holl K, Honnay O, Hornstein D, Hou E, Hough-Snee N, Hovstad KA, Ichie T, Igić B, Illa E, Isaac M, Ishihara M, Ivanov L, Ivanova L, Iversen CM, Izquierdo J, Jackson RB, Jackson B, Jactel H, Jagodzinski AM, Jandt U, Jansen S, Jenkins T, Jentsch A, Jespersen JRP, Jiang G-F, Johansen JL, Johnson D, Jokela EJ, Joly CA, Jordan GJ, Joseph GS, Junaedi D, Junker RR, Justes E, Kabzems R, Kane J, Kaplan Z, Kattenborn T, Kavelenova L, Kearsley E, Kempel A, Kenzo T, Kerkhoff A, Khalil MI, Kinlock NL, Kissling WD, Kitajima K, Kitzberger T, Kjøller R, Klein T, Kleyer M, Klimešová J, Klipel J, Kloeppel B, Klotz S, Knops JMH, Kohyama T, Koike F, Kollmann J, Komac B, Komatsu K, König C, Kraft NJB, Kramer K, Kreft H, Kühn I, Kumarathunge D, Kuppler J, Kurokawa H, Kurosawa Y, Kuyah S, Laclau J-P, Lafleur B, Lallai E, Lamb E, Lamprecht A, Larkin DJ, Laughlin D, Le Bagousse-Pinguet Y, le Maire G, le Roux PC, le Roux E, Lee T, Lens F, Lewis SL, Lhotsky B, Li Y, Li X, Lichstein JW, Liebergesell M, Lim JY, Lin Y-S, Linares JC, Liu C, Liu D, Liu U, Livingstone S, Llusià J, Lohbeck M, López-García Á, Lopez-Gonzalez G, Lososová Z, Louault F, Lukács BA, Lukeš P, Luo Y, Lussu M, Ma S, Maciel Rabelo Pereira C, Mack M, Maire V, Mäkelä A, Mäkinen H, Malhado ACM, Mallik A, Manning P, Manzoni S, Marchetti Z, Marchino L, Marcilio-Silva V, Marcon E, Marignani M, Markesteijn L, Martin A, Martínez-Garza C, Martínez-Vilalta J, Mašková T, Mason K, Mason N, Massad TJ, Masse J, Mayrose I, McCarthy J, McCormack ML, McCulloh K, McFadden IR, McGill BJ, McPartland MY, Medeiros JS, Medlyn B, Meerts P, Mehrabi Z, Meir P, Melo FPL, Mencuccini M, Meredieu C, Messier J, Mészáros I, Metsaranta J, Michaletz ST, Michelaki C, Migalina S, Milla R, Miller JED, Minden V, Ming R, Mokany K, Moles AT, Molnár A, Molofsky J, Molz M, Montgomery RA, Monty A, Moravcová L, Moreno-Martínez A, Moretti M, Mori AS, Mori S, Morris D, Morrison J, Mucina L, Mueller S, Muir CD, Müller SC, Munoz F, Myers-Smith IH, Myster RW, Nagano M, Naidu S, Narayanan A, Natesan B, Negoita L, Nelson AS, Neuschulz EL, Ni J, Niedrist G, Nieto J, Niinemets Ü,

Nolan R, Nottebrock H, Nouvellon Y, Novakovskiy A, Nystuen KO, O'Grady A, O'Hara K, O'Reilly-Nugent A, Oakley S, Oberhuber W, Ohtsuka T, Oliveira R, Öllerer K, Olson ME, Onipchenko V, Onoda Y, Onstein RE, Ordonez JC, Osada N, Ostonen I, Ottaviani G, Otto S, Overbeck GE, Ozinga WA, Pahl AT, Paine CET, Pakeman RJ, Papageorgiou AC, Parfionova E, Pärtel M, Patacca M, Paula S, Paule J, Pauli H, Pausas JG, Peco B, Penuelas J, Perea A, Peri PL, Petisco-Souza AC, Petraglia A, Petritan AM, Phillips OL, Pierce S, Pillar VD, Pisek J, Pomogaybin A, Poorter H, Portsmuth A, Poschlod P, Potvin C, Pounds D, Powell AS, Power SA, Prinzing A, Puglielli G, Pyšek P, Raevel V, Rammig A, Ransijn J, Ray CA, Reich PB, Reichstein M, Reid DEB, Réjou-Méchain M, de Dios VR, Ribeiro S, Richardson S, Riibak K, Rillig MC, Riviera F, Robert EMR, Roberts S, Robroek B, Roddy A, Rodrigues AV, Rogers A, Rollinson E, Rolo V, Römermann C, Ronzhina D, Roscher C, Rosell JA, Rosenfield MF, Rossi C, Roy DB, Royer-Tardif S, Rüger N, Ruiz-Peinado R, Rumpf SB, Rusch GM, Ryo M, Sack L, Saldaña A, Salgado-Negret B, Salguero-Gomez R, Santa-Regina I, Santacruz-García AC, Santos J, Sardans J, Schamp B, Scherer-Lorenzen M, Schleuning M, Schmid B, Schmidt M, Schmitt S, Schneider JV, Schowanek SD, Schrader J, Schrodt F, Schuldt B, Schurr F, Selaya Garvizu G, Semchenko M, Seymour C, Sfair JC, Sharpe JM, Sheppard CS, Sheremetiev S, Shiodera S, Shipley B, Shovon TA, Siebenkäs A, Sierra C, Silva V, Silva M, Sitzia T, Sjöman H, Slot M, Smith NG, Sodhi D, Soltis P, Soltis D, Somers B, Sonnier G, Sørensen MV, Sosinski Jr EE, Soudzilovskaia NA, Souza AF, Spasojevic M, Sperandii MG, Stan AB, Stegen J, Steinbauer K, Stephan JG, Sterck F, Stojanovic DB, Strydom T, Suarez ML, Svenning J-C, Svitková I, Svitok M, Svoboda M, Swaine E, Swenson N, Tabarelli M, Takagi K, Tappeiner U, Tarifa R, Tauugourdeau S, Tavsanoglu C, te Beest M, Tedersoo L, Thiffault N, Thom D, Thomas E, Thompson K, Thornton PE, Thuiller W, Tichý L, Tissue D, Tjoelker MG, Tng DYP, Tobias J, Török P, Tarin T, Torres-Ruiz JM, Tóthmérész B, Treurnicht M, Trivellone V, Trolliet F, Trotsiuk V, Tsakalos JL, Tsiripidis I, Tysklind N, Umehara T, Usoltsev V, Vadeboncoeur M, Vaezi J, Valladares F, Vamosi J, van Bodegom PM, van Breugel M, Van Cleemput E, van de Weg M, van der Merwe S, van der Plas F, van der Sande MT, van Kleunen M, Van Meerbeek K, Vanderwel M, Vanselow KA, Vårhammar A, Varone L, Vasquez Valderrama MY, Vassilev K, Vellend M, Veneklaas EJ, Verbeeck H, Verheyen K, Vibrans A, Vieira I, Villacís J, Violle C, Vivek P, Wagner K, Waldram M, Waldron A, Walker AP, Waller M, Walther G, Wang H, Wang F, Wang W, Watkins H, Watkins J, Weber U, Weedon JT, Wei L, Weigelt P, Weiher E, Wells AW, Wellstein C, Wenk E, Westoby M, Westwood A, White PJ, Whitten M, Williams M, Winkler DE, Winter K, Womack C, Wright IJ, Wright SJ, Wright J, Pinho BX, Ximenes F, Yamada T, Yamaji K, Yanai R, Yankov N, Yguel B, Zanini KJ, Zanne AE, Zelený D, Zhao Y-P, Zheng J, Zheng J, Ziemińska K, Zirbel CR, Zizka G, Zo-Bi IC, Zotz G, Wirth C (2020) TRY plant trait database – enhanced coverage and open access. Global Change Biology 26(1): 119–188. https://doi.org/10.1111/gcb.14904

Király G [Ed.] (2007) Vörös Lista- a magyarországi edényes flóra veszélyeztetett fajai [Red list of the vascular flora of Hungary]. Sopron, 73 pp.

Király G [Ed.] (2009) Új magyar fűvészkönyv. Magyarország hajtásos növényei. Határozókulcsok. [New Hungarian Herbal. The Vascular Plants of Hungary. Identification key.]. Aggteleki Nemzeti Park Igazgatóság, Jósvafő, 628 pp.

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: A database of life-history traits of the Northwest European flora. Journal of Ecology 96(6): 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Lakatos M, Bihari Z, Hoffmann L, Izsák B, Kircsi A, Szentimrey T (2018) Observed climate change in Hungary 1901–2016 [in Hungarian]. OMSZ - Hungarian Meteorological Service Webpage. https://www.met.hu/eghajlat/eghajlatvaltozas/megfigyelt_valtozasok/Magyarorszag/

Leht M (2005) Cladistic and phenetic analyses of relationships in *Vicia* subgenus *Cracca* (Fabaceae) based on morphological data. Taxon 54(4): 1023–1032. https://doi.org/10.2307/25065486

Lesku B, Molnár A (2007) A Hortobágy növényritkaságai. Daru füzetek, Hortobágyi Nemzeti Park Igazgatóság, Debrecen.

Lyons KG, Schwartz MW (2001) Rare species loss alters ecosystem function - invasion resistance. Ecology Letters 4(4): 358–365. https://doi.org/10.1046/j.1461-0248.2001.00235.x

Lyons KG, Brigham CA, Traut BHH, Schwartz MW (2005) Rare species and ecosystem functioning. Conservation Biology 19: 1019–1024. https://doi.org/10.1111/j.1523-1739.2005.00106.x

Marini L, Bruun HH, Heikkinen RK, Helm A, Honnay O, Krauss J, Kühn I, Lindborg R, Pärtel M, Bommarco R (2012) Traits related to species persistence and dispersal explain changes in plant communities subjected to habitat loss. Diversity & Distributions 18(9): 898–908. https://doi.org/10.1111/j.1472-4642.2012.00893.x

Metz J, Liancourt P, Kigel J, Harel D, Sternberg M, Tielbörger K (2010) Plant survival in relation to seed size along environmental gradients: A long-term study from semi-arid and Mediterranean annual plant communities. Journal of Ecology 98(3): 697–704. https://doi.org/10.1111/j.1365-2745.2010.01652.x

Molnár VA, Molnár A, Vidéki R, Pfeiffer N, Gulyás G (2000) Néhány adat Magyarország flórájának ismeretéhez. Kitaibelia 5: 297–303.

Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J, Thuiller W (2013) Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. PLoS Biology 11: e1001569. https://doi.org/10.1371/journal.pbio.1001569

Newton R, Hay F, Probert R (2014) Royal Botanic Gardens, Kew Protocol for comparative seed longevity testing. https://brahmsonline.kew.org/Content/Projects/msbp/resources/Training/01-Comparative-longevity.pdf

Oleas NH, Peterson CL, Thompson J, Richardson ML, Reynaldo Y, Von Wettberg EJB (2018) Genetic and habitat variation among populations of the critically imperiled *Vicia ocalensis* (Fabaceae) in the Ocala National Forest, USA. The Journal of the Torrey Botanical Society 145(3): 202–211. https://doi.org/10.3159/TORREY-D-16-00064.1

Pake E, Venable DL (1996) Seed Banks in Desert Annuals : Implications for Persistence and Coexistence in Variable Environments. Ecology 77(5): 1427–1435. https://doi.org/10.2307/2265540

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918): 37–42. https://doi.org/10.1038/nature01286

Pence VC, Meyer A, Linsky J, Gratzfeld J, Pritchard HW, Westwood M, Bruns EB (2022) Defining exceptional species—A conceptual framework to expand and advance ex situ conservation of plant diversity beyond conventional seed banking. Biological Conservation 266: 109440. https://doi.org/10.1016/j.biocon.2021.109440

Philippi T (1993) Bet-hedging germination of desert annuals: Variation among populations and maternal effects in *Lepidium lasiocarpum*. American Naturalist 142(3): 488–507. https://doi.org/10.1086/285551

Pimm SL, Jones HL, Diamond J (1988) On the Risk of Extinction. American Naturalist 132(6): 757–785. https://doi.org/10.1086/284889

POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. http://www.plantsoftheworldonline.org/

Probert RJ, Daws MI, Hay FR (2009) Ecological correlates of ex situ seed longevity: A comparative study on 195 species. Annals of Botany 104(1): 57–69. https://doi.org/10.1093/aob/mcp082

R Core Team (2019) R: A Language and Environment for Statistical Computing. https://www.r-project.org/

Renzi JP, Chantre GR, Cantamutto MA (2014) Development of a thermal-time model for combinational dormancy release of hairy vetch (*Vicia villosa* ssp. *villosa*). Crop & Pasture Science 65(5): 470. https://doi.org/10.1071/CP13430

Rubio de Casas R, Willis CG, Pearse WD, Baskin CC, Baskin JM, Cavender-Bares J (2017) Global biogeography of seed dormancy is determined by seasonality and seed size: A case study in the legumes. The New Phytologist 214(4): 1527–1536. https://doi.org/10.1111/nph.14498

Saatkamp A, Cochrane A, Commander L, Guja LK, Jimenez-Alfaro B, Larson J, Nicotra A, Poschlod P, Silveira FAO, Cross AT, Dalziell EL, Dickie J, Erickson TE, Fidelis A, Fuchs A, Golos PJ, Hope M, Lewandrowski W, Merritt DJ, Miller BP, Miller RG, Offord CA, Ooi MKJ, Satyanti A, Sommerville KD, Tangney R, Tomlinson S, Turner S, Walck JL (2019) A research agenda for seed-trait functional ecology. The New Phytologist 221(4): 1764–1775. https://doi.org/10.1111/nph.15502

Sala OE, Chapin FS, Armesto JJ, Berlow EL, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global Biodiversity Scenarios for the Year 2100. Source: Science, New Series 287: 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Salisbury EJ (1942) The reproductive capacity of plants. Studies in quantitative biology. G. Bell & Sons, London, UK, 244 pp.

Säterberg T, Jonsson T, Yearsley J, Berg S, Ebenman B (2019) A potential role for rare species in ecosystem dynamics. Scientific Reports 9: 11107. https://doi.org/10.1038/s41598-019-47541-6

Schindler S, O'Neill FH, Biró M, Damm C, Gasso V, Kanka R, van der Sluis T, Krug A, Lauwaars SG, Sebesvari Z, Pusch M, Baranovsky B, Ehlert T, Neukirchen B, Martin JR, Euller K, Mauerhofer V, Wrbka T (2016) Multifunctional floodplain management and biodiversity effects: A knowledge synthesis for six European countries. Biodiversity and Conservation 25(7): 1349–1382. https://doi.org/10.1007/s10531-016-1129-3

Somlyay L, Bauer N (2013) Adatok a *Vicia biennis* L. elterjedéséhez a Pannonicum-ban. Kitaibelia 18: 125–128.

Sonkoly J, Deák B, Valkó O, Molnár VA, Tóthmérész B, Török P (2017) Do large-seeded herbs have a small range size? The seed mass–distribution range trade-off hypothesis. Ecology and Evolution 7(24): 11204–11212. https://doi.org/10.1002/ece3.3568

Sonkoly J, Tóth E, Balogh N, Balogh L, Bartha D, Bata K, Bátori Z, Békefi N, Botta-Dukát Z, Bölöni J, Csecserits A, Csiky J, Csontos P, Dancza I, Deák B, Dobolyi ZK E-Vojtkó A, Gyulai F, Hábenczyus AA, Henn T, Horváth F, Höhn M, Jakab G, Kelemen A, Király G, Kis S, Kovacsics-Vári G, Kun A, Lehoczky É, Lengyel A, Lhotsky B, Löki V, Lukács BA, Matus G, McIntosh-Buday A, Mesterházy A, Miglécz T, Molnár V. A, Molnár Z, Morschhauser T, Papp L, Pósa P, Rédei T, Schmidt D, Szmorad F, Takács A, Tamás J, Tiborcz V, Tölgyesi C, Tóth K, Tóthmérész B, Valkó O, Virók V, Wirth T, Török P

(2022) PADAPT 1.0–the Pannonian Database of Plant Traits (preprint). https://doi.org/10.1101/2022.12.05.519136

Soó R (1980) A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve I-VI. Akademiai Kiado Rt., Budapest.

Sőth Á (2017) Két hazai védett növény csírázási tulajdonságai és ex-situ védelmének helyzete. BSc Thesis, Állatorvostudományi Egyetem, Budapest, Hungary.

Stohlgren TJ, Bull KA, Otsuki Y, Villa CA, Lee M (1998) Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology 138(1): 113–125. https://doi.org/10.1023/A:1009764909413

Tapiquén CEP (2015) Hydrography of Europe. Based on shapes from Enviromental Systems Research Institute (ESRI). Free Distribuition. Orogénesis Soluciones Geográficas. Porlamar, Venezuela.

Thompson K (1993) Seed persistence in soil. In: Henry GAF, Grime JP (Eds) Methods in comparative plant ecology. Springer, Dordrecht, 199–202.

Thompson K, Band SR, Hodgson JG (1993) Seed size and shape predict persistence in soil. Functional Ecology 7(2): 236. https://doi.org/10.2307/2389893

Thompson K, Bakker JP, Bekker RM, Hodgson JG (1998) Ecological correlates of seed persistence in soil in the north-west European flora. Journal of Ecology 86(1): 163–169. https://doi.org/10.1046/j.1365-2745.1998.00240.x

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102(23): 8245–8250. https://doi.org/10.1073/pnas.0409902102

Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9(3-4): 137–152. https://doi.org/10.1016/j.ppees.2007.09.004

Van Assche JA, Vandelook FEA (2010) Combinational dormancy in winter annual Fabaceae. Seed Science Research 20(4): 237–242. https://doi.org/10.1017/S0960258510000218

Venable DL, Brown JS (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. American Naturalist 131(3): 360–384. https://doi.org/10.1086/284795

Violle C, Jiang L (2009) Towards a trait-based quantification of species niche. Journal of Plant Ecology 2(2): 87–93. https://doi.org/10.1093/jpe/rtp007

Violle C, Navas M, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116(5): 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle C, Reich PB, Pacala SW, Enquist BJ, Kattge J (2014) The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences of the United States of America 111(38): 13690–13696. https://doi.org/10.1073/pnas.1415442111

Volis S, Bohrer G (2013) Joint evolution of seed traits along an aridity gradient: Seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. The New Phytologist 197(2): 655–667. https://doi.org/10.1111/nph.12024

Westoby M (1981) How Diversified Seed Germination Behavior is Selected. American Naturalist 118(6): 882–885. https://doi.org/10.1086/283880

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33(1): 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Zhang X, Mosjidis JA (1995) Breeding systems of several *Vicia* species. Crop Science 35(4): 1200–1202. https://doi.org/10.2135/cropsci1995.0011183X003500040049x